

THE LARVAL DEVELOPMENT OF THE COMMENSAL
CRAB POLYONYX GIBBESI Haig, 1956
(CRUSTACEA: DECAPODA)^{1, 2}

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The larvae of the anomuran crab family Porcellanidae have long been recognized in the plankton by their unique rostral spine (Thompson, 1836). Until recently, however, there was little attempt to rear the larvae in the laboratory under controlled conditions through their complete life cycle. To date, adequate descriptions of the complete larval development are available for species of *Pachycheles* (Kurata, 1964; Knight, 1966; Boschi *et al.*, 1967), *Petrocheles* (Wear, 1965a, 1966), *Petrolisthes* (Gohar and Al Kholly, 1957; Wear, 1964 a, b, 1965b; Greenwood, 1965) *Pisidia* (formerly some *Porcellana* species; Lebour, 1943; Bourdillon-Casanova, 1956), *Porcellana* (Lebour, 1943; Bourdillon-Casanova, 1960) and *Polyonyx* (Knight, 1966).

Polyonyx gibbesi, which is found from Woods Hole, Massachusetts to La Paloma, Uruguay, is a known commensal with the polychaete worm *Chaetopterus variopedatus* (Renier) (see Pearse, 1913; Gray, 1961 and Haig, 1966). Faxon (1879, 1882) briefly described and figured the first and second zoea and the "first stage of the crab" (= megalopa) of *Polyonyx macrocheles* Gibbes (now called *Polyonyx gibbesi* Haig 1956). Faxon's figures and descriptions are unfortunately not sufficiently detailed to allow positive identification of the larvae or comparison with larvae of other species of *Polyonyx*. A second author (MacArthur, 1962, unpublished) also described the larval development of *Polyonyx macrocheles* (sic) but differences between the larvae she studied and mine will require further study before an evaluation can be made.

The purpose of this paper is to illustrate and describe the complete larval development of *Polyonyx gibbesi*. Certain characters are discussed which may enable the larvae of the genus to be identified from the plankton. The relationship between *P. gibbesi* and the Pacific coast form *Polyonyx quadriungulatus* is also discussed.

MATERIALS AND METHODS

Ovigerous female *Polyonyx* were collected from *Chaetopterus* tubes obtained by bucket dredge in the Cape Florida Channel, from an area 3 m. deep and

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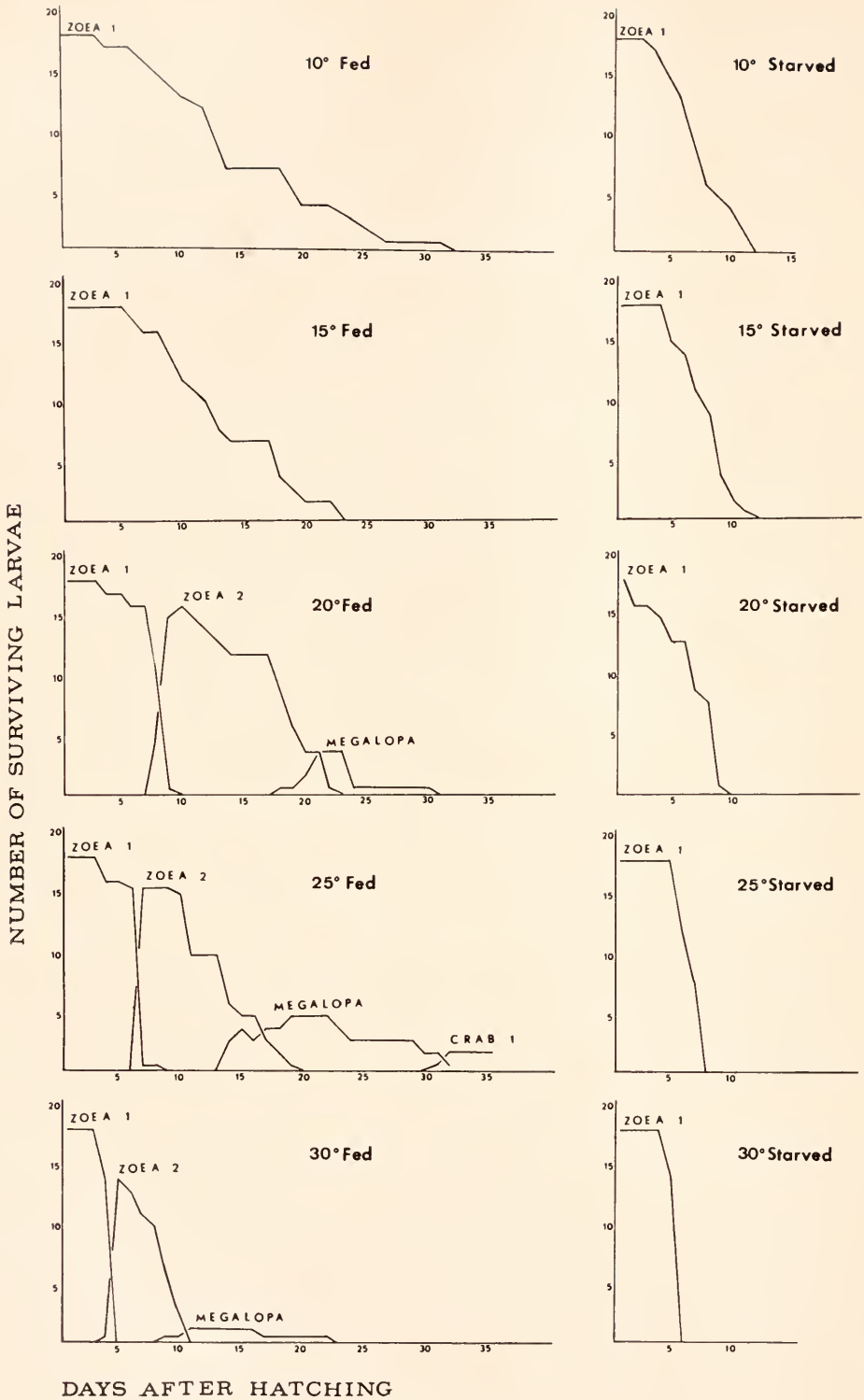


FIGURE 1.

20 m. offshore of Hurricane Harbor, Key Biscayne, Florida. The crabs were isolated in non-flowing sea water in 19-cm. diameter plastic bowls until hatching occurred. Zoeae were placed, one each, in compartmented plastic tackle boxes. Each compartment held about 40 cc. of unfiltered sea water (33–35‰ salinity). Two series of boxes, one with zoeae fed with *Artemia salina* nauplii, and one with starved zoeae, were maintained at 10°, 15°, 20°, 25°, and 30° C. Temperature variation was not more than $\pm 1.5^\circ$ C. Larvae were fed and received a change of water every other day. Illumination was not controlled. A record was kept for all molts and deaths for each larva, with exuviae and dead larvae preserved in 70% ethanol. Larvae obtained from another female were held at 25° C. ($\pm 2^\circ$ C.) and several zoeae were sacrificed every day, and also preserved in 70% ethanol. Appendages were dissected in 40% lactic acid and mounted in Turtox CMC-S. Illustrations were made with a camera lucida attached to a Wild M-20 binocular compound microscope, from slides of individual appendages. Drawings were checked both for accuracy and individual larval variation against appendages dissected from exuviae and sacrificed animals. Measurements were made with a LaFayette objective micrometer. Carapace length was measured from the anterior margin of the zoeal eye to the insertion of the posterior spines on the zoeal carapace, and from the edge of the megalopal frontal region to the posterior margin of the carapace for carapace length, and across the widest part of the carapace for carapace width. The carapace measurements provided are the arithmetic average of 10 specimens measured in each larval stage. One spent female (UMML 32:3581) plus hatched specimens of first and second zoeae and megalopae (UMML 32:3582) were placed in the Museum of the Institute of Marine Sciences.

RESULTS

Polyonyx gibbesi passes through a pre-zoeal stage, two zoeal stages and one megalopal stage. As noted for other porcellanids (*e.g.* Knight, 1966) there is an increase in size of the third maxillipeds, gills and pleopods during the zoeal stages. Some authors (*e.g.* Boschi *et al.*, 1967) consider this increase a substage, though no molt is seen. Others (*e.g.* Boyd and Johnson, 1963) refer to molting that produces additional stages but little or no alteration of form as substages. The term substage needs re-definition. I never observed exuviae other than the two zoeal molts, and I do not use the term substage.

Temperature noticeably affects larval development, altering the duration of each stage or preventing the development to subsequent stages. Figure 1 depicts the length of time the larvae, both fed and starved, spent in each stage at various temperatures. No starved zoeae developed beyond the first stage. Fed zoeae at 10° and 15° C. remained in Stage I, living at 10° C. for a maximum of 32 days, and at 15° C. for a maximum of 22 days, before dying. Animals reared at 20°, 25°, and 30° C. reached the megalopal stage in a minimum of 18, 14 and eight days, respectively. Crab stages were obtained only at 25° C. While the

FIGURE 1. *Polyonyx gibbesi*: Duration of survival in each stage of larval development, fed and starved, at various temperatures. Horizontal scale represents the number of days after hatching. The vertical scale represents the number of surviving larvae. Salinity range = 33–35‰.

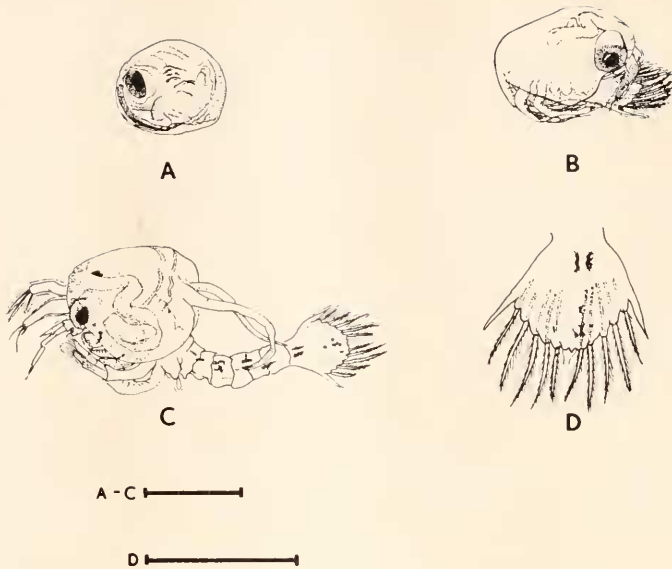


FIGURE 2. *Polyonyx gibbsi*: pre-zoea. A. Larva in egg just before hatching. B. Larva in process of hatching. C. Newly hatched pre-zoea. Remnants of pre-zoeal cuticle surround appendages. Rostral spine and setae on appendages not yet emerged. D. Pre-zoeal telson. Two hairs on central prominence of telson and other fine setae not yet present. Scales equal 0.5 mm.

shortest duration of development occurred at 30° C., no crab stages were obtained. Mortality at this temperature was very high and only three zoeae molted to megalopa and none of these survived longer than 11 days. Thus, 25° C. allowed the best development in the temperature series. At this temperature the first and second zoeal stages lasted six to seven days and the megalopal stage usually lasted 12 to 14 days.

DESCRIPTION OF THE LARVAE

Pre-zoea

The hatching sequence of the entire egg mass lasted about two hours (see Fig. 2, A, B). The pre-zoeal stage also lasts about two hours. The long rostral spine, in the pre-zoea as yet undeveloped, is partially bent outside and under the carapace and partially invaginated into the carapace above the midgut region (Fig. 2, C). The embryonic cuticle in the specimens examined was almost completely fragmented. Setae on the appendages and telson, only partly extruded at the beginning of the stage, become completely extruded toward the end of the stage. The setae on the carapace over the eyes and setae on the central prominence of the telson (Fig. 2, D) are not present. The pre-zoeae swim by rapid abdominal flexion.

In two instances pre-zoeae swam from *Chaetopterus* tubes maintained in the laboratory. If the larvae did not hatch as pre-zoeae they might encounter difficulty in escaping through the narrow neck of the worm tube.

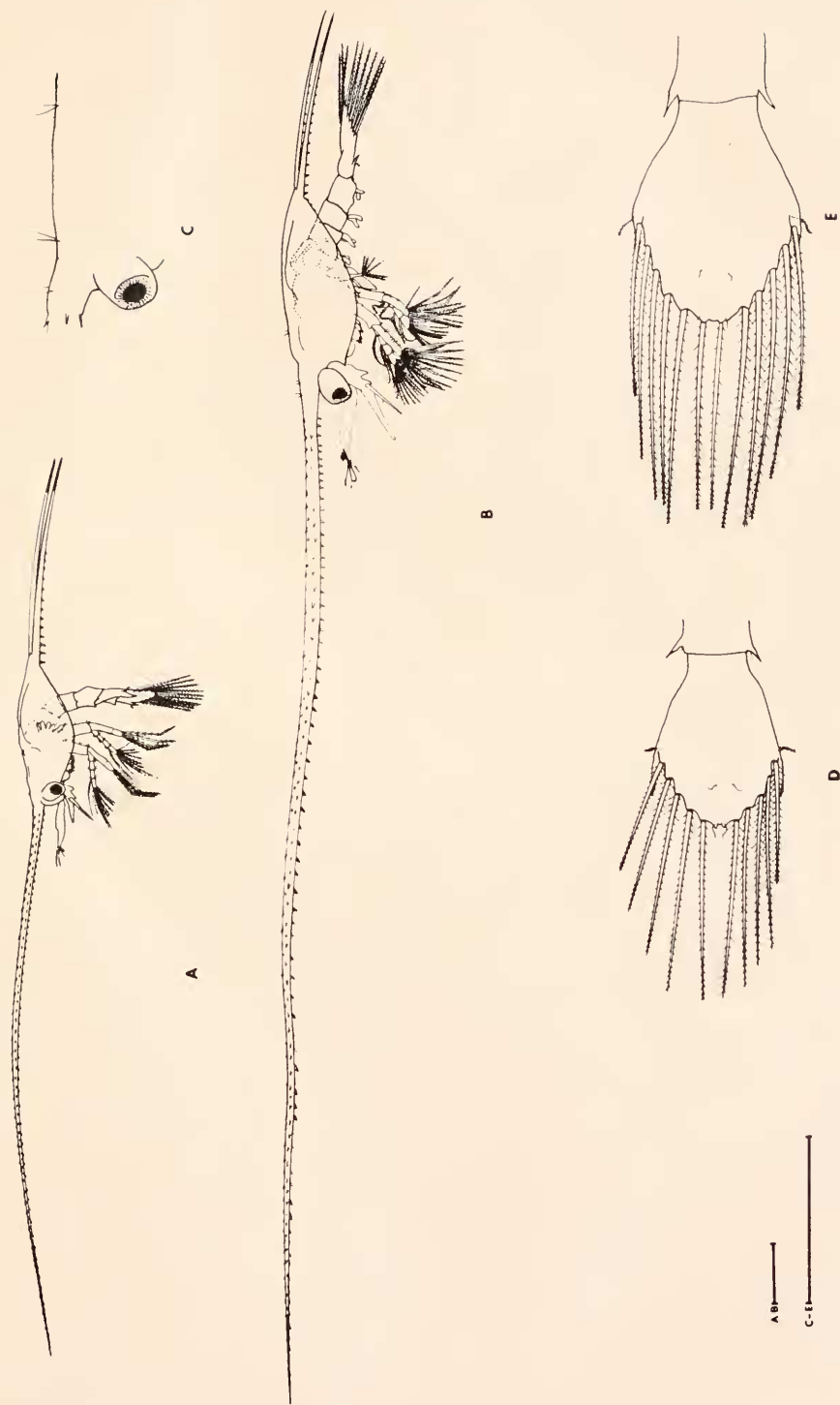


FIGURE 3. *Polyonyx gibbesi*: first and second zoeal stages. A, First zoea. B, Second zoea. C, Caparapace of first zoea showing dorsal setae. D, Telson of second zoea. E, Telson of first zoea. Scales equal 0.5 mm.

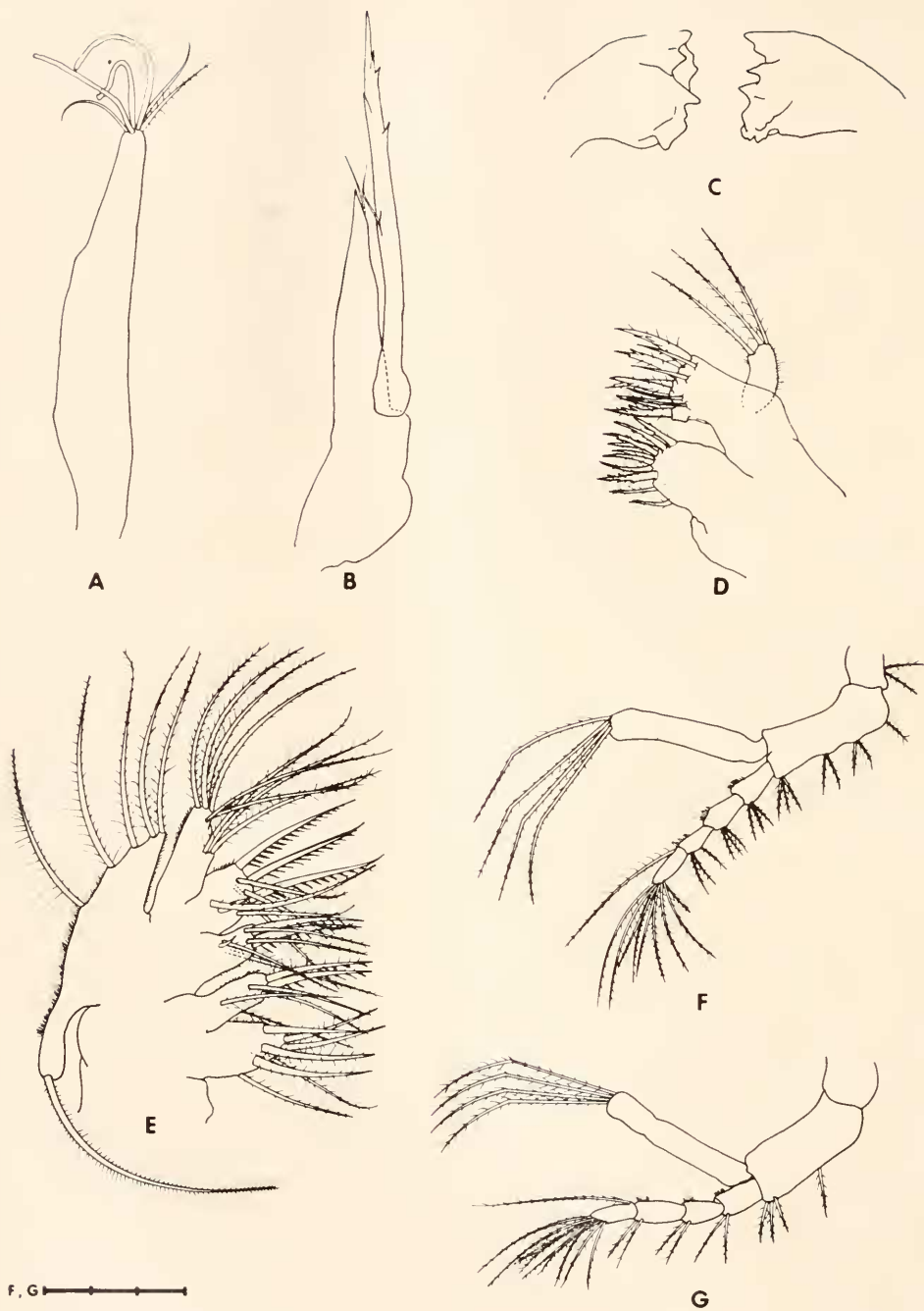


FIGURE 4. *Polyonyx gibbesi*; first zoeal appendages. A. Antennule. B. Antenna. C. Mandibles. D. Maxillule. E. Maxilla. F. Maxilliped 1. G. Maxilliped 2. Scales equal 0.3 mm.

First Zoea

Carapace length: 1.2 mm.

Number of specimens examined: 20

Carapace (Fig. 3, A). Typically porcellanid, produced anteriorly into an extremely long rostral spine up to seven times the length of carapace proper; posteriorly into two straight or divergent posterior carapace spines 1.4 to 1.8 times as long as carapace. Armature of spines as illustrated. Curvature of rostral and posterior carapace spines variable, depending in part on frequency of collision by new zoeae with other objects.

Dorsal surface of carapace with three pairs of fine setae. Placement illustrated in Figure 3, C.

Antennule: (Fig. 4, A). A simple slightly flabelliform rod with two long and one short aesthetasc and two or three setae of variable length, one with fine setules.

Antennae: (Fig. 4, B). Endopodite, fused to protopodite, has a thin subterminal seta. Exopodite a thin spine almost twice as long as endopodite; about six small spinelets distally plus a thin seta halfway down its length.

Mandibles: (Fig. 4, C). Asymmetrical dentate processes without palp.

Maxillule: (Fig. 4, D). Endopodite unsegmented, 3 setae. Coxal and basal endites each with 10 processes as shown.

Maxilla: (Fig. 4, E). Endopodite unsegmented, 4 terminal, two subterminal and three medial setae. Coxal endite with seven processes on proximal lobe, six on distal lobe. Basal endite with seven processes on proximal lobe, nine on distal lobe. Scaphognathite with five setae laterally and one long apical plumose seta. Placement of all setae as illustrated.

Maxilliped 1: (Fig. 4, F). Four and ten setae on terminal segments of exopodite and endopodite, respectively. Basipodite setation progressing distally is 1, 2-3, 2, 3. Small tufts of hair dorsally on endopodite segments one to three.

Maxilliped 2: (Fig. 4, G). Setation on terminal segments similar to maxilliped 1. Basipodite setation 1-2, 3 progressing distally. Tufts of hair dorsally on segments one to three of endopodite as in maxilliped 1.

Maxilliped 3: (Fig. 3, A). A small bifid lobe, with one or two setae.

Pereiopods: Five buds visible in most specimens; extremely small and distorted in early stage. Both buds and maxilliped 3 increase in size as zoea progresses to Stage II.

Abdomen: (Fig. 3, A). Five somites, each with lateral spine of increasing length on somites nearer the telson. Somites three and four may each have a fine hair dorso-laterally; somite five has two fine setae just above lateral spine on each side.

Pleopods: Absent. Primordia visible in some zoeae from the plankton.

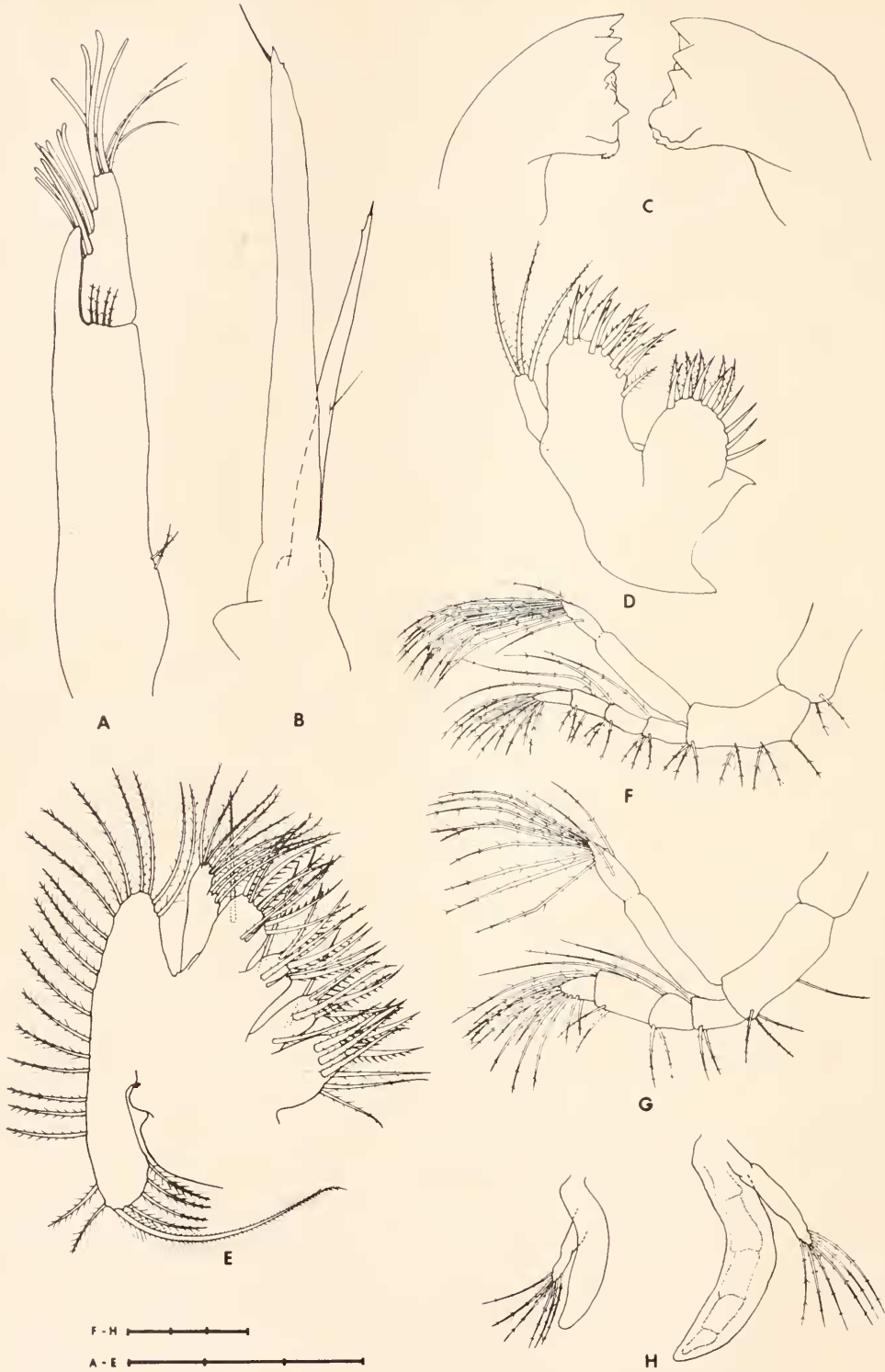


FIGURE 5.

Telson: (Fig. 3, D). Distinctive characters are minutely serrated lateral spines, the thin seta next to each telson spine, two fine hairs on central prominence, minute serrations terminally on articulated plumose setae, and two fine hairs medially on dorsal surface of telson proper. Anal spine present.

Color: Zoea transparent with red-orange chromatophores as follows: dorsally and ventrally surrounding the gut throughout abdomen; dorsally between lateral spines on telson; dorsally on tip of telson; interiorly around mouthparts. Rostral spine diffusely red-orange at tip and intermittently so throughout its length; posterior carapace spines diffusely red-orange only at tips.

Second zoea

Carapace length: 1.7 mm.

Number of specimens examined: 15

Carapace: (Fig. 3, B). Three pairs of dorsal setae persist. Rostral spine about six times carapace length; posterior spines of carapace up to 1.6 times carapace length. Spination on ventral margin of posterior spines may extend onto carapace in some zoeae.

Antennule: (Fig. 5, A). Biramous; exopodite with three or four long aesthetascs and four terminal setae, one seta plumose. Subterminal aesthetascs arranged in three groups as 2, 3, 3 progressing proximally. Endopodite slightly less than half the length of exopodite. At junction of exopodite and endopodite are four small setae; two additional setae on basal medial projection of protopodite.

Antenna: (Fig. 5, B). Similar to Stage I. Exopodite now about $\frac{2}{3}$ as long as endopodite; distal spination almost absent.

Mandibles: (Fig. 5, C). Larger, with three or four teeth and smaller dentate processes. No evidence of palp though Faxon (1879) reported one present and illustrated it as rudiment.

Maxillule: (Fig. 5, D). Endopodite setation same as in Stage I. Coxal and basal endites with 12 processes each, as illustrated. One late stage zoea with one more seta on lateral margin of coxal endite making 13 processes.

Maxilla: (Fig. 5, E). Endopodite setation same as Stage I. Coxal endite with 17-18 setae, 10 on proximal lobe, seven or eight on distal lobe. Basal endite with nine setae on proximal lobe, 11 on distal lobe. Scaphognathite retains apical plumose seta, and now has about 24 setae on margins.

Maxilliped 1, 2: (Fig. 5, F-G). Terminal segments of exopodite and endopodite with about 12 setae. Dorsal tuft of hairs on endopodite segments replaced by single long seta on each segment. Third segment of endopodite of Maxilliped 2 much swollen and nearly twice as long as other segments. Other setation similar to Stage I.

FIGURE 5. *Polyonyx gibbsi*; second zoeal appendages. A. Antennule. B. Antenna. C. Mandibles. D. Maxillule. E. Maxilla. F. Maxilliped 1. G. Maxilliped 2. H. Maxilliped 3, early (l.) and late (r.) stage. Scales equal 0.3 mm.

Maxilliped 3: (Fig. 5, H). Exopodite indistinctly segmented with six terminal setae. Endopodite, the same length or slightly longer than exopodite after molting, increases in length throughout second stage. It measures three times the length of exopodite just before molt to megalopa.

Pereiopods: One and five indistinctly chelate. Gills present. Pereiopods and gills enlarge noticeably throughout duration of Stage II. Toward end of Stage II the almost completely formed pereiopods are tucked under posterior portion of carapace.

Pleopods: (Fig. 3, B). Buds present, of decreasing length on abdominal segments two through five. Buds increase in size as stage progresses.

Telson: (Fig. 3, E). Now with two long articulated plumose setae on central prominence making 8 + 8 processes. Fine hairs below prominence and those adjacent to lateral spines are retained. Setation on dorsal surface unchanged from Stage I.

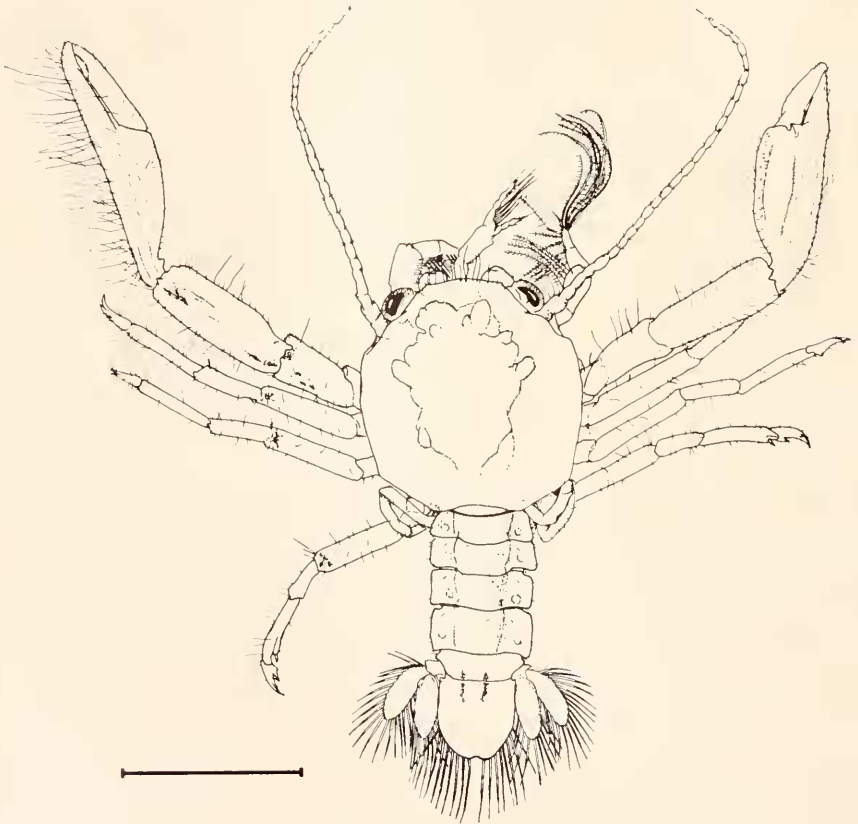


FIGURE 6. *Polyonyx gibbsi*; megalopa. Right antennule and left maxilliped 3 removed for clarity. Scale line equals 1 mm.

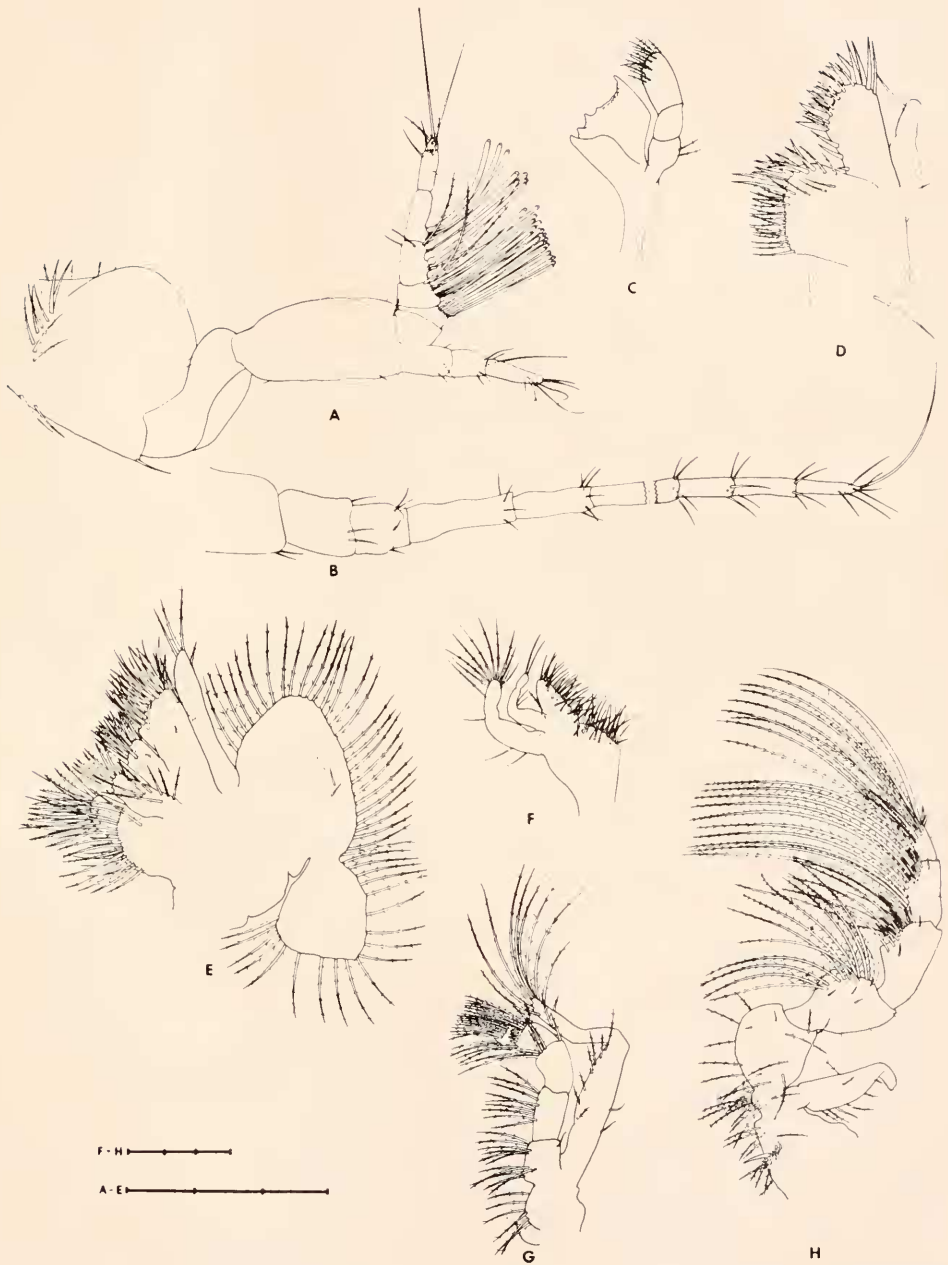


FIGURE 7. *Polyonyx gibbesi*; megalopal appendages. A. Antennule (less tips of aesthetascs). B. Antenna (in part). C. Mandible. D. Maxillae. E. Maxilla. F. Maxilliped 1. G. Maxilliped 2. H. Maxilliped 3. Scales equal 0.3 mm.

Color: Chromatophore distribution and color similar to Stage I. As zoea approaches molt to megalopa, rostral spine becomes completely orange. Posterior spines of carapace colored orange but to lesser extent.

Megalopa

The megalopa (Fig. 6) resembles the adult crab closely, enough so that Faxon (1879, 1882) considered it the "first stage of the crab." And, though he acknowledged the presence of biramous pleopods on the abdomen, to substantiate his belief he also cited a lack of persistent zoeal characters expected to appear in a megalopa stage. Because of this, at least one author (*e.g.*, Williams, 1965: 114) has quoted Faxon's error without further evaluation.

Chelae are well developed and fringed with setae on their outer margin. The juvenile and adult crab is always broader than long whereas only in the megalopa are the animals longer than broad. Carapace width-to-length measurements ranged from 1.2 mm. \times 1.2 mm. to 1.4 mm. \times 1.4 mm. First crab measurements were 1.8 mm. wide by 1.6 mm. long.

Carapace: (Fig. 6). Rounded or somewhat quadrate. Frontal region little produced; bears numerous setae. Eyes relatively large compared to first crab stage.

Antennule: (Fig. 7, A). Biramous, with three-segmented peduncle; basal segment enlarged. Lower ramous three-segmented; upper ramous has seven segments with aesthetascs on segments two through five in the following sequence of rows and numbers: one row (10), two rows (10, 3, +2 setae), two rows (3, 2, +1 seta), one row (3). Other setation on both rami as illustrated.

Antenna: (Fig. 7, B). Three-segmented peduncle plus 25 short segments, each bearing several short setae. Terminal segment usually with a long seta.

Mandibles: (Fig. 7, C). Three-segmented palp present, first segment has two setae on distal edge; distal segment with approximately 15–20 strong setae and spines.

Maxillule: (Fig. 7, D). Endopodite two-segmented, with setae as shown. Basal and coxal endites have approximately 29 and 36 processes, respectively, placed as shown.

Maxilla: (Fig. 7, E). Endopodite unsegmented; three or four terminal, two or rarely three subterminal setae. Proximal lobe of coxal endite with at least 10 and up to 13 terminal processes, three subterminal processes and about 20 setae in a ring around middle of lobe. Distal lobe with six or seven terminal and three subterminal processes; seven setae progress down its side. Proximal lobe of basal endite with about 15 processes; distal lobe has about 30. Scaphognathite has 48 or more plumose setae around edge.

Maxilliped 1: (Fig. 7, F). Setation fragile and variable; exopodite with two to ten setae; endopodite with four to six setae; protopodite with 50 or more setae on coxal and basal lobes.

Maxilliped 2: (Fig. 7, G). Exopodite elongate, about 20 setae on its two segments. Setation on four-segmented endopodite progressing distally is 9, 8, 18–20,

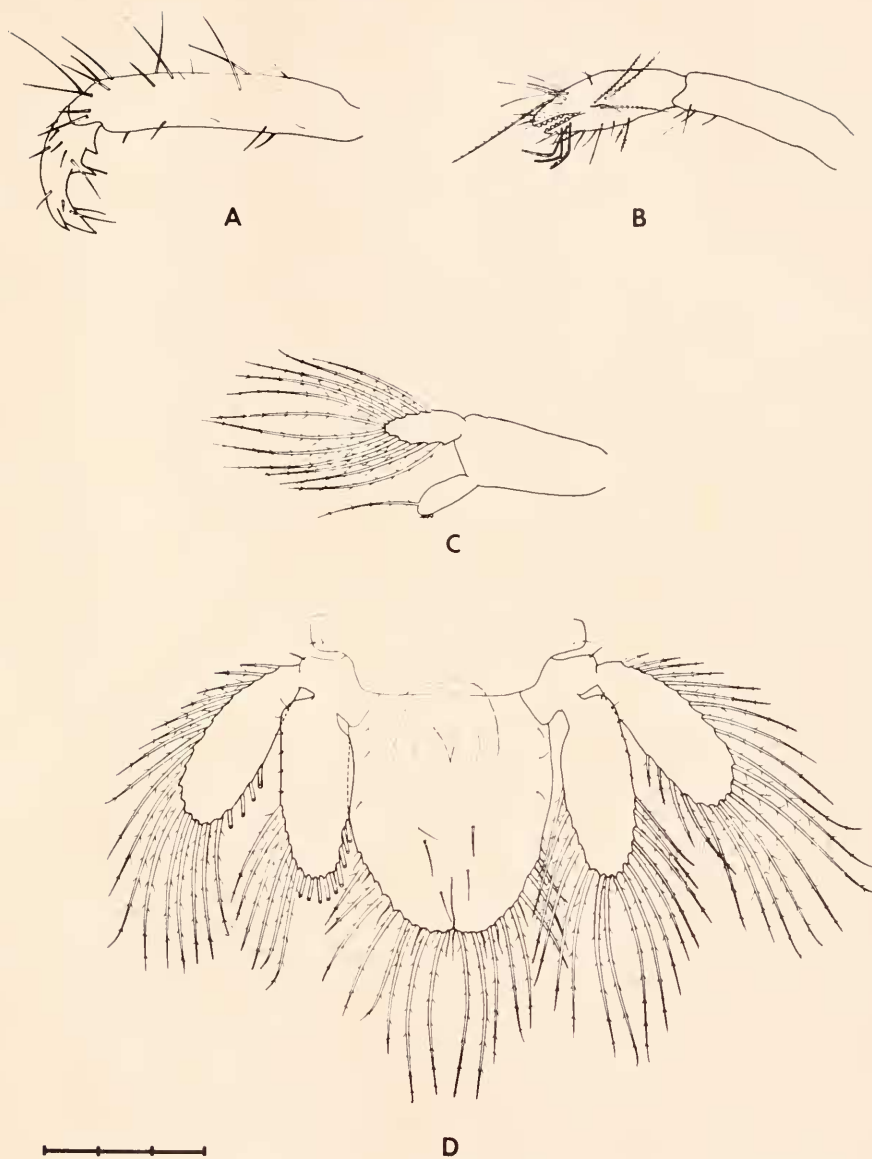


FIGURE 8. *Polyonyx gibbesi*; locomotory appendages of megalopa. A. Pereiopod 2. B. Pereiopod 5. C. Pleopod. D. Tail-Fan. Scale equals 0.3 mm.

about 18. Basipodite and coxopodite with about six and 12 setae, respectively. Placement as illustrated.

Maxilliped 3: (Fig. 7, H). Numerous setae on inner margin of basal lobes; about 14 setae and small spine on coxal lobe, as shown. Processes on five-segmented endopodite as follows: ischium, about 14; merus, about 16; carpus, about 18; pro-

podus, about 23; dactylus, about 15. Ischium, merus and carpus have thin, plate-like extensions. Exopodite has six to eight setae, placed as illustrated.

Pereiopods: (Fig. 6; 8 A, B). Chelipeds large, flattened, subequal, somewhat distorted, covered with setae. Walking legs setose, with two small blunt spines on distal edge of propodus (spines may be poorly developed); dactyl with three or four accessory spines. Pereiopod five chelate, gape appearing dentate in some, approximately 25 setae and three pectinate scythe-like hooks near gape.

Pleopods: (Fig. 8, C). Biramous, of decreasing size on abdominal somites nearer the telson. Exopodites with usually 12 setae; endopodites with one subterminal seta and an appendix interna.

Telson: (Fig. 8, D). 8 + 8 plumose setae plus additional spines and setae as

TABLE I
Comparison of zoeal appendages in two species of *Polyonyx*.
Data for *P. quadriungulatus* from Knight (1966)
and for *P. gibbesi* from the present work.

Appendage	Zoea I		Zoea II	
	<i>P. gibbesi</i>	<i>P. quadriungulatus</i>	<i>P. gibbesi</i>	<i>P. quadriungulatus</i>
ANTENNULE Exopodite Endopodite	Simple rod 3 aesthetascs; 2-3 setae	Simple rod 3 aesthetascs; 3 setae	Biramous 11 aesthetascs; 4 setae 1/2 length of exopodite	Biramous 11 aesthetascs; 4 setae 1/2 length of exopodite
ANTENNA Exopodite Endopodite	Biramous 2 × length of endopodite; spinous	Biramous 3 × length of endopodite; spinous	Similar to Stage I 2/3 length of endopodite Spination reduced As in Stage I	Similar to Stage I About equal to endopodite Spination as in Stage As in Stage I
MANDIBLE	Asymmetrical simple processes	Asymmetrical simple processes	3 large teeth No palp	2 teeth figured No palp
MAXILLULE Endopodite Coxal endite Basal endite	3 apical setae 4 spines; 6 setae 6 spines; 4 setae	3 apical setae 4 spines; 6 setae 6 spines; 4 setae	3 setae 5 spines; 7 setae 7 spines; 5 setae	3 setae 5 spines; 7 setae 7 spines; 5 setae
MAXILLA Endopodite Coxal endite Basal endite Scaphognathite	9 setae 13 processes 16 processes 5 setae; 1 spine	9 setae 13 processes 16 processes 5 setae; 1 spine	9 setae 17-18 processes 20-21 processes 24 (+1 apical) setae	9 setae 17 processes 20 processes 21-26 (+1 apical) setae
MAXILLIPED 1 Coxopodite Basipodite Endopodite Exopodite	2 setae 1.2-3.2,3, setae 3,3,10 setae 4 natatory setae	2 setae 1,2,2,3 setae 3,3,3,8 setae 4 natatory setae	2 setae 1,2,2,3 setae 4,4,4,12 setae 12 setae	2 setae 1,2,2,3 setae 4,4,4,9 setae 11-12 setae
MAXILLIPED 2 Coxopodite Basipodite Endopodite Exopodite	1 seta or naked 1-2,3 setae 2,2,2,10 setae 4 natatory setae	Naked 1,2 setae 2,2,2,8 setae 4 natatory setae	1 seta or naked 1,3 setae 3,3,3,12 setae 12 setae	Naked 1,2 setae 3,3,3,9 setae 11-14 setae
MAXILLIPED 3 Endopodite Exopodite	Small bifid lobe	Rudimentary	Now functional Increases in length 2 indistinct segments; 6 setae	Now functional Increases in length 2 indistinct segments; 6 setae
PEREIOPODS	Present as buds	Present as buds	Developing Chelation seen Chelation seen	Developing Chelation seen Chelation seen
ABDOMEN	5 somites with lateral spines	5 somites with lateral spines	Pleopod buds present Increase in size seen	Pleopod buds present Increase in size seen
TELSON	7 + 7 processes; 2 hairs on central prominence	7 + 7 processes; 2 hairs on central prominence	8 + 8 processes, hairs on prominence retained	8 + 8 processes, hairs on prominence retained

shown. Uropods biramous, exopodites with 18–24, endopodites 12–16, setae around distal margins.

DISCUSSION

At present the complete larval development is known for only two of the 23 described species of *Polyonyx*, one from the eastern Pacific and one from the western Atlantic. A comparison between the eastern Pacific *Polyonyx quadriungulatus* and *P. gibbesi* shows that the zoeal stages are almost exactly similar in number and placement of setae (see Table I). *P. gibbesi* differs most notably in having more setae on the terminal segments of the endopodites of the maxillipeds in both zoeal stages (10 and 12) than *P. quadriungulatus* (8 and 9). Only detailed examination of each appendage reveals further differences between the zoeae of the two species (e.g., different number of setae and spines on the second maxillae).

More easily observed is the relative length of the antennal exopodite to the endopodite in the two species (see Table I). Knight (1966) considered this a good character for distinguishing *P. quadriungulatus* from *Porcellana* and *Pisidia*, the two other members of Lebour's (1943) triad relationship. It is also possible on this basis to separate *P. gibbesi* from *P. quadriungulatus*. In the latter the antennal exopodite is three times the length of the endopodite in Stage I zoea, becoming about equal to the endopodite in Stage II. In *P. gibbesi* the antennal exopodite is only twice as long as the endopodite in Stage I and becomes $\frac{2}{3}$ the length of the endopodite in Stage II. Thus, the exopodite is always shorter in the zoeal stages of *P. gibbesi* than in *P. quadriungulatus*.

A third character which distinguishes *P. gibbesi* from *P. quadriungulatus* is seen in the dorsal setation of the zoeal carapace. The eastern Pacific form has but two setae in both zoeal stages while *P. gibbesi* has three pairs in both stages. Setae on the dorsal surface of the telson, often difficult to observe, may be an additional feature to separate larvae of the two species.

Differences in the megalopae of the two species are less distinct. The mouthparts are quite similar in both form, and number and placement of setae. A comparison of the megalopae in Table II shows that detailed examination is again necessary to separate the two forms. In general, however, *P. gibbesi* has more setae on the mouthparts than *P. quadriungulatus*. It also lacks both the two small spines at the bases of long setae and the articulated spines on the posterior distal margin of the propodus which *P. quadriungulatus* possesses.

The adult morphology of the two species is quite similar. Haig (1960, p. 239) stated that "Aside from *Polyonyx nitidus* Lockington, *P. quadriungulatus* is most closely related to . . . *P. gibbesi*." Further, both *P. gibbesi* and the two California species just mentioned belong to Johnson's (1958) "*P. sinensis* group" (Haig, 1960, p. 238). This group is a complex of species from the Indo-Pacific (and now including California to Panama, the eastern U. S., and the west African coast, Haig, *in litt.*) which show similar morphology, plus "a pronounced tendency toward commensalism" (Johnson, 1958, p. 97). *P. gibbesi* is considered an obligate commensal with the polychaete worm *Chaetopterus variopedatus* (Gray, 1961), the megalopa establishing the initial relationship with the worm (Gore, unpublished data). Both California species have been found commensal with *Chaetopterus* though they may not be obligate commensals.

TABLE II
Comparison of megalopa appendages in two species of Polyonyx.
Data for P. quadrangulatus from Knight (1966)
and for P. gibbesi from the present work.

Appendage	<i>P. gibbesi</i>	<i>P. quadrangulatus</i>	Appendage	<i>P. gibbesi</i>	<i>P. quadrangulatus</i>
ANTENNULE	Biramous 3 segmented peduncle, basal segment en- larged 3 segments 7 segments; 10, 10 + 3, 3 + 2, 3 aes- thetasc in tiers	Biramous 3 segmented peduncle, basal segment en- larged 3 segments 7 segments; 10, 10 + 3, 3 + 2, 3 aes- thetasc in tiers	MAXILLIPED 2 Propodite Endopodite	18 setae 4 segments; 9, 8, 18- 20, 18 setae (in tufts on segs. 3-4)	10 setae* 4 segments; —, 8, in tufts, in tufts
Ventral ramus	3 segments	3 segments	Exopodite	2 segments; 11 termi- nal, 9 marginal setae	2 segments; 11 terminal, 7 marginal setae
Dorsal ramus	7 segments; 10, 10 + 3, 3 + 2, 3 aes- thetasc in tiers	7 segments; 10, 10 + 3, 3 + 2, 3 aes- thetasc in tiers	MAXILLIPED 3 Propodite	Serrated spine, numer- ous setae	Serrated tooth, numer- ous setae
ANTENNA	About 25 segments 3 segmented peduncle Small lobe on first peduncular segment	About 30 segments 3 segmented peduncle Small cylindrical branch on first pe- duncular segment	Endopodite	5 segments; about 14, 17, 21, 27, 17 processes	5 segments; 15, 14, 20, 12, ? processes*
MANDIBLE	3 segmented palp About 20 setae	3 segmented palp 15-17 setae	Exopodite	6 terminal, 6 marginal setae	6 terminal, 6 marginal* setae
MAXILLULE	2 segments; 1-2 setae 14 spines, 15 setae 10 spines, 26 setae	2 segments; 1-2 setae 10 spines, 21 setae* About 44 processes*	PEREIOPODS 2-4	Dactyls with 3-4 hooks; propodus may have 2 small spines distally	Dactyls with 4 fixed hooks; propodus with 2 articulated spines
Basal endite	Unsegmented, 7 setae 45 processes 49 processes About 47 setae	Unsegmented, 8 setae 41 processes* 43 processes* 48-58 setae	PEREIOPOD 5	Chelate; 26 setae + 3 scythe-like hooks	Chelate; 1 spine, 2-3 scythe-like hooks + setae
Coxal endite	50 or more setae 6-7 setae 10 or 11 setae	About 50 setae 7 setae 13-20 setae	PLEOPODS 1-4 Endopodites Exopodites	1 subterminal seta; +5 terminal hooks Usually 12 setae	1 subterminal seta; 4-5 terminal hooks 12, 12-13, 13, 13 setae
Scaphognathite			UROPODS Endopodite Exopodite	10-12 setae 18-22 setae	10-13 setae 17-22 setae
MAXILLIPED 1 Propodite Endopodite Exopodite			TELESON	8 + 8 plumose setae, + spines	8 + 8 plumose setae, + spines

The similarity in adult and larval morphology, the geographical isolation between Pacific and Atlantic forms, plus the similarity in commensal habitat indicates that *P. gibbesi* and *P. quadriungulatus* are geminate species. Thus they are one more species pair of the many that are known to exist between Caribbean-Atlantic and Pacific coast forms (e.g., *Minyocerus kirki* and *angustus*, *Porcellana cancri-socialis* and *sayana*, etc., see Haig, 1960).

Lebour (1943) thought that Faxon's *Polyonyx macrocheles* would fit into the *Porcellana*- (and *Pisidia*) -*Polyonyx* complex, distinguished chiefly by the placement of the fifth plumose setae of the telson in the first and second zoeal stages. Knight (1966) showed that *Polyonyx quadriungulatus* adhered to Lebour's scheme and the present work confirms Lebour's suggestion for *P. gibbesi* (formerly *P. macrocheles*). The differences in antennal proportions between *Porcellana-Pisidia* and *Polyonyx quadriungulatus*, as noted by Knight (see above), apply also to *P. gibbesi*. Thus, the zoeal features such as spined antennal exopodite and its length relative to both the antennal endopodite and to the antennule allow *P. gibbesi* to be separated from *P. quadriungulatus* in both zoeal stages, as already discussed, and from the known species of *Porcellana* and *Pisidia* in the first zoeal stage. The scheme breaks down in the second zoeal stage since, in *P. gibbesi*, the antennal exopodite is $\frac{2}{3}$ as long as the endopodite while the endopodite is about as long as the antennule proper. *Polyonyx gibbesi* thus shows antennal characters (in length) similar to those shown by known species of *Porcellana* and *Pisidia* in the second zoeal stage.

The previously mentioned carapace setation may, however, allow complete separation of *Polyonyx gibbesi* in both zoeal stages from *Porcellana-Pisidia* zoeae. If it is consistent in other members of the genus *Polyonyx* then, together with the features mentioned above, it would make *Polyonyx* larvae immediately distinguishable from most other porcellanid larvae. The value of this last character must await further studies on the larvae of other genera since some western Atlantic species of *Pachycheles*, *Petrolisthes*, *Porcellana* and *Minyocerus* also have dorsal carapacial setation (Gore, unpublished data). Studies are presently being carried out on the larvae of other genera of Porcellanidae from the south Florida and Caribbean area. Each of the genera mentioned has good distinguishing features in the zoeae which, in conjunction with Lebour's characters regarding the telson, may allow them to be separated from one another (Gore, unpublished data). As larvae of these genera become better known it will be possible to construct a key for their identification and to clarify the relationships between them.

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SUMMARY

1. The larval development of the porcellanid crab, *Polyonyx gibbesi*, a commensal with the polychaete worm *Chaetopterus variopedatus*, is described and illustrated. Two series of larvae were hatched and maintained in the laboratory, one fed with *Artemia* nauplii and the other starved. Members of each series were held at 10°, 15°, 20°, 25° and 30° C. At 25° C. the fed larvae hatched as pre-zoeae and molted through two additional zoeal stages to the megalopa. Duration of the pre-zoeal stage is about two hours, each of the zoeal stages usually lasts six to seven days and the megalopa lasts 12–14 days before molting to first crab. No crab stages were obtained above or below 25° C. and no megalopae were obtained below 20° C. Starved larvae died before attaining Stage II.

2. Comparison of the larvae of *Polyonyx gibbesi* with those of *Polyonyx quadriungulatus*, an eastern Pacific species, shows the zoeae and megalopae to be almost identical both in appendages and in form, numbers, and placement of setae. Similarity of morphology and habitat plus geographical isolation indicate that *P. gibbesi* and *P. quadriungulatus* are geminate species.

3. Larvae of *Polyonyx gibbesi* possess certain features which allow them to be recognized in the plankton as well as distinguished from known larvae of genera of other western Atlantic porcellanid crabs.

LITERATURE CITED

- BOSCHI, E. E., M. A. SCELZO AND B. GOLDSTEIN, 1967. Desarrollo larval de dos especies de Crustaceos Decapodos en el laboratorio. *Pachycheles haigae* Rodrigues Da Costa (Porcellanidae) y *Chasmagnathus granulata* Dana (Grapsidae). *Bol. Inst. Biol. mar. Univ. nac. B. Aires*, (12): 1–46.
- BOURDILLON-CASANOVA, L., 1956. Note sur la présence de *Porcellana bluteli* (Risso) Alvarez dans le Golfe de Marseille et sur le développement larvaire de cette espèce. *Rapp. P.-v. Reun. Comm. int. Explor. scient. Mer Mediterr.*, 13: 225–232.
- BOURDILLON-CASANOVA, L., 1960. Le meroplanchton du Golfe de Marseille: Les larves de crustacés décapodes. *Recl. Trav. Stn. mar. Endoume, Fasc. 30, Bull.*, 18: 1–286.
- BOYD, C. M., AND M. W. JOHNSON, 1963. Variations in the larval stages of a decapod crustacean, *Pleuroncodes planipes* Stimpson (Galatheidae). *Biol. Bull.*, 124: 141–152.
- FAXON, W., 1879. On some young stages in the development of *Hippa*, *Porcellana* and *Pinnixa*. *Bull. Mus. Comp. Zool., Harv.*, 5: 253–268.
- FAXON, W., 1882. Selections from embryological monographs. I. Crustacea. *Mem. Mus. Comp. Zool., Harv.*, 9 (1), 14 pls.
- GOHAR, H. A. F., AND A. A. AL KHOLY, 1957. The larvae of four decapod Crustacea (from the Red Sea). *Publs. Mar. Biol. Stn. Ghardaqa*, 9: 177–202.
- GRAY, I. E., 1961. Changes in abundance of the commensal crabs of *Chaetopterus*. *Biol. Bull.*, 120: 353–359.
- GREENWOOD, J. G., 1965. The larval development of *Petrolisthes elongatus* (H. Milne Edwards) and *Petrolisthes novaezelandae* Filhol (Anomura, Porcellanidae) with notes on breeding. *Crustaceana*, 8: 285–307.
- HAIG, J., 1960. The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. *Rep. Allan Hancock Pac. Exped.*, 24: 1–440.
- HAIG, J., 1966. Porcellanid Crabs (Crustacea Anomura). *Résult. scient. Camp. Calypso, Fasc. 7*: 351–358.
- JOHNSON, D. S., 1958. The Indo-West Pacific species of the genus *Polyonyx* (Crustacea, Decapoda, Porcellanidae). *Ann. Zool., Agra*, 2: 95–118.
- KNIGHT, M. D., 1966. The larval development of *Polyonyx quadriungulatus* Glassell and *Pachycheles rudis* Stimpson (Decapoda, Porcellanidae) cultured in the laboratory. *Crustaceana*, 10: 75–97.

- KURATA, H., 1964. Larvae of decapod Crustacea of Hokkaido. 7. Porcellanidae (Anomura). *Bull. Hokkaido Reg. Fish. Res. Lab.*, 29: 66-70.
- LEBOUR, M. V., 1943. The larvae of the genus *Porcellana* (Crustacea, Decapoda) and related forms. *J. Mar. Biol. Assoc.*, 25: 721-737.
- MACARTHUR, C. L., 1962. Larval development of the commensal crab *Polyonyx macrocheles*. Unpublished Master's thesis, Duke University, 40 pp.
- PEARSE, A. S., 1913. On the habits of the crustaceans found in *Chaetopterus* tubes at Woods Hole, Massachusetts. *Biol. Bull.*, 24: 102-114.
- THOMPSON, J. V., 1836. Memoir on the metamorphosis in *Porcellana* and *Portunus*. *The Entomological Magazine*, 3: 275-280.
- WEAR, R. G., 1964a. Larvae of *Petrolisthes novaezealandae* Filhol, 1885 (Crustacea, Decapoda, Anomura). *Trans. Roy. Soc. N. Z.*, 4: 229-244.
- WEAR, R. G., 1964b. Larvae of *Petrolisthes elongatus* (Milne Edwards, 1837) (Crustacea, Decapoda, Anomura). *Trans. Roy. Soc. N. Z.*, 5: 39-53.
- WEAR, R. G., 1965a. Larvae of *Petrocheles spinosus* Miers, 1876 (Crustacea, Decapoda, Anomura) with keys to New Zealand porcellanid larvae. *Trans. Roy. Soc. N. Z.*, 5: 147-168.
- WEAR, R. G., 1965b. Breeding cycles and pre-zoea larva of *Petrolisthes elongatus* (Milne Edwards, 1837) (Crustacea, Decapoda). *Trans. Roy. Soc. N. Z.*, 5: 169-175.
- WEAR, R. G., 1966. Pre-zoea larva of *Petrocheles spinosus* Miers, 1876 (Crustacea, Decapoda, Anomura). *Trans. Roy. Soc. N. Z.*, 8: 119-124.
- WILLIAMS, A. B., 1965. Marine decapod crustaceans of the Carolinas. *Fishery Bull. Fish Wildl. Serv. U. S.*, 65: 1-298.